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NOTE ON AN EXPERIMENTAL PROBLEM OF THE LATE A. G. WEBSTER

By F. L. Hitchcock

Department of Mathematics, Massachusetts Institute of Technology

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In a letter dated January 15, 1923 Professor Webster described in the following terms a problem in which he had long been interested:

"The problem is described on page 223 of Volterra's *Fonctions de Lignes*, where he has credited me with much more than I deserve, because whereas we have made loads of experiments in the last twelve years, we do not yet know whether the theory is verified, because we have not been able to solve the integral equation. The conditions of the problem lead to the integro-differential equation

$$d^2T/dt^2 + m^2\,[T + \int_0^t \psi(\xi)T(t-\xi)d\xi] = 0 \qquad (1)$$

in which ψ is the heredity function. It is to be noticed that from physical reasons this is to be a monotonically decreasing function, and presumably has no points of inflection. We might reasonably assume it to be composed of a finite or infinite number of terms of the form

$$\psi(t) = \Sigma\, a_r e^{-b_r t}. \qquad (2)$$

The object of the experiment being to find the form of this function, the bar is set vibrating and its damping observed. This gives us the form of T which is a simple harmonic function $\cos \alpha t$ multiplied by a damping factor $f(t)$."

In later conversation Professor Webster explained to me that the damping factor $f(t)$ agreed very well with the empirical formula

$$f(t) = \frac{1}{e^{\beta t} - \gamma} \qquad (3)$$

in all his experiments. He thus assumed

$$T(t) = \frac{\cos \alpha t}{e^{\beta t} - \gamma} \qquad (4)$$

By differentiation the equation (1) may be thrown into the form

$$\psi(t) + (1 - \gamma) \int_0^t T'(t - \xi)\psi(\xi)d\xi = (\gamma - 1)T'''/m^2 + (\gamma - 1)T' \quad (5)$$

which is an integral equation in the Volterra form. The values of the constants α, β, and γ were empirically determined in each experiment. Employing the hypotheses (2) and (3), several mathematicians had carried out an investigation and had agreed, so Professor Webster said, in the opinion that some or all of the exponents b_r must be imaginary, a result which appeared to him incompatible with the physical facts of the case.

Being much interested in the problem, I suggested that, in view of the fact that the formula (3) was empirical, the question was primarily concerned with the numerical data rather than with a formal solution, and that a function $\psi(t)$ might exist which should satisfy (5) within the limits of experimental error and yet not agree in form with the solution rigorously deduced from the hypothesis (3). If this approximate solution should prove to be independent of the constant α, that is, independent of the particular rate of vibration of the bar in a given experiment, it would go a long way toward establishing the theory. He agreed that this would be an important result, and very kindly gave me as a sample set of data

$$\alpha = 171.4, \beta = 0.02028, \gamma = 0.6574.$$

By the rather elementary process of assuming a power series for ψ, instead of (2), I then determined the approximate solution of (5)

$$\psi(t) = C_0 + C_1 t + C_2 t^2 \quad (6)$$

where

$$C_0 = \frac{-\beta^3 h + 3\beta^3 h^2}{-\alpha^2 - \beta^2 h + 2\beta^2 h^2} - 2\beta h \quad (7)$$

in which for brevity I have put

$$h = \frac{1}{1 - \gamma} \quad (8)$$

while C_1 is found to be

$$C_1 = \frac{-\beta^4 h + 8\beta^4 h^2 - 13\beta^4 h^3 + 4\beta^4 h^4}{-\alpha^2 - \beta^2 h + 2\beta^2 h^2} - 4\beta^2 h + 6\beta^2 h^2 \quad (9)$$

and C_2 similarly

$$2C_2 = \frac{\beta^5(-h + 19h^2 - 72h^3 + 71h^4 - 16h^5)}{-\alpha^2 - \beta^2 h + 2\beta^2 h^2} - 8\beta^3 h + 40\beta^3 h^2 - 34\beta^3 h^3. \quad (10)$$

In these results the constant α is present, to be sure, but enters only as α^2 and only in the denominator. Since α^2 is large compared with the other quantities concerned, it follows that the fractions on the right of (7), (9), and (10) are negligibly small, or that the solution is actually independent of the constant α.

While this outcome based on a single set of data is not conclusive, it is suggestive, and was pleasing to Professor Webster. He promised to send me the entire set of observations in order that I might determine, if possible, another empirical formula which should differ but little numerically from (3) but should be of a form leading to a solution rigorously independent of α; and if this should not be possible, to see if the solution given by equations (6)–(10) would in all cases be in good agreement with the data. No doubt he would have carried out this promise if he had lived.

A NEW KIND OF REPRESENTATION OF SURFACES

By G. Y. Rainich

Department of Mathematics, Johns Hopkins University

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In a paper[1] after having outlined the theory of surfaces in a purely vectorial form and indicated how the usual method of representation arises from the orthogonal projection we put the question whether there is a possibility of other representations. In this paper we will discuss one of these.

We imagine, first of all, a curve Σ and an axis Π in a plane. Through a point A of Σ we draw two unit vectors: one p perpendicular to Π and the other a normal to Σ; we form their sum $p + a$ and we multiply this new vector with a number σ which we chose so that the tip of the resulting vector $\sigma.(p + a)$ lies on the axis Π; with other words we draw the bissectrix of the angle between the perpendicular to Π and the normal to Σ in the point A to the intersection with the axis Π. This intersection or the tip of the vector $\sigma.(p + a)$ we consider as the generalized sterographical projection of A relative to the curve Σ. We introduce now on Π a fixed point O and characterize all the points of Π by their distances x from this point (their abscissae). The number σ is a function of x and the form of this function depends upon the shape of the curve just as the form of the function which shows how the ordinate depends on the abscissa gives the shape of the curve in the ordinary Cartesian representation.

The function $\sigma(x) = a + bx$ gives in our case a straight line and every

straight line can be represented in this form with finite values of the coefficients; the function $\sigma(x) = a + bx + cx^2$ represents a circle with the radius

$$(b^2 - 4ac + 1)/4c. \qquad (1)$$

If we expand in the more general case the function $\sigma(x)$ in a power series

$$\sigma(x) = a + b(x - \alpha) + c(x - \alpha)^2 + d(x - \alpha)^3 + \ldots$$

the first two terms $a + b(x - \alpha)$ represent the tangent line and the first three terms $a + b(x - \alpha) + c(x - \alpha)^2$ — the osculating circle, so that the curvature can be expressed rationally in the first and second derivatives of $\sigma(x)$, unlike the usual representation, but we will not dwell on this case any longer.

Given a curved surface Σ and a plane Π we can use a similar projection by drawing in each point A of Σ two unit vectors: one p perpendicular to the plane Π and the other a normal to the surface Σ and forming the vector $\sigma.(p + a)$ with the tip on Π. In the case when Σ is a sphere tangent to Π this gives the known stereographic projection which justifies the term generalized stereographic projection which we use for the more general thing.

Let us consider a vector x_A of the bundle A (*loc. cit.*, p. 180); if we project its tip along a line parallel to that which projects the point A, the projections of these two points determine on Π a vector which we will call the generalized sterographic projection of x_A. It is a very important fact that the length of the projected vector is the same as the length of the projection and that, more generally, the product of two vectors of the same bundle is preserved in this operation.

As the representation of a tensor $\varphi(A, x_A, y_A \ldots)$ belonging to the surface we take the tensor of the plane Π which makes to correspond to the projections of the vectors $x_A, y_A \ldots$ the same number as the original tensor makes to correspond to these vectors. In the case of gen. stereographic projection which we use throughout the paper the representation of a tensor differs from the tensor represented only by its location in space, so that it has the same invariants etc., unlike again the usual representation where tensors are distorted with the exception of eventually one point (for which the system of coördinates is geodetic).

We can introduce coördinates in the plane Π and characterize the points of the surface by the coördinates of the points of Π which are their projections. Having in mind the representation of the vicinity of a point P we take as the plane Π the tangent plane in P and we use rectangular axes with the origin in P; we may call the resulting system of representation of points of Σ "Cartesian semi-coördinates." A vector x_A will be represented in this system by the components of its stereographic projection and, according to what was said before, the length of the vector with the

components x_1, x_2 will be $\sqrt{x_1^2 + x_2^2}$; the product of two vectors with the components x_1, x_2 and y_1, y_2 will be $x_1y_1 + x_2y_2$; a tensor will be represented by a multilinear form or by its coefficients as usual but all the algebraic operations such as contraction, formation of invariants will be performed in the same simple way as if the curvature would be zero in all points or as if we would use for each point geodetic coördinates. The question of transformation of these semi-coördinates seems to be a very interesting if not a very simple one.

We will consider now some questions of analysis. We denote by x_{AB} the vector of the bundle B which is the (gen. sterogr.) projection of x_A on the tangent plane in B. The operation so defined gives us the same services as the operation which transforms x_A into $x_{A.B}$ which we used in the previous paper in giving the definition of the differential of a tensor-field, but it has the advantage that we don't need to consider two operations of this kind: the two relations (12) of the previous paper are replaced here by the simpler relations.

$$x_{APA} = x_A \text{ and } x_{AP} \cdot y_{AP} = x_A \cdot y_A. \tag{2}$$

We consider now the question which in the usual representation is the origin of the absolute differential, viz. given the representation of a tensor to find the representation of its differential. In order to be better understood I will state the results in coördinate (or rather semi-coördinate) form, although I obtained them originally using vectors in pure form. If we have a tensor field φ of the rank zero the representation of its differential is

$$\frac{\partial \varphi}{\partial x_i} + \sigma s_{ij} \frac{\partial \varphi}{\partial x_j}; \tag{3}$$

if we have a tensor field φ_i of the first rank the representation of its differential is

$$\frac{\partial \varphi_i}{\partial x_j} + \sigma s_{jk} \frac{\partial \varphi_i}{\partial x_k} + \Gamma_{k,ij} \varphi_k \tag{4}$$

and so on; here σ has the meaning explained above, s_{ij} are the coefficients of the form which represents the tensor $s(h)$ and

$$\Gamma_{k,ij} = \frac{\partial \sigma}{\partial x_i} s_{jk} - \frac{\partial \sigma}{\partial x_k} s_{ij}. \tag{5}$$

We see that the analysis is here rather more complicated than in the usual representation but the differentiation does not involve the metric which seems to be an advantage.

[1] These PROCEEDINGS, 9, No. 6, pp. 179–83. June, 1923.

THE ELECTROMAGNETIC FIELD AND CURVATURE

BY G. Y. RAINICH

DEPARTMENT OF MATHEMATICS, JOHNS HOPKINS UNIVERSITY

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Every theory of curved space is a generalization of the theory of surfaces; but the direction in which the generalization is made depends upon the form in which the original theory is presented; the direction in which Riemann generalized the theory of surfaces was determined by the fact that he took as the starting point the Gaussian theory of surfaces based on the form of the linear element and this fact determined to a great degree the development of theoretical physics during the last decade. We will try to build a theory of curved space generalizing the theory of surfaces in a slightly different direction.[1] We will take as our starting point the intrinsic theory as it was outlined in our first paper.[2]

Since the most important thing—the only fundamental tensor indeed—in this theory is the tensor $\delta(h, k) = s(h) \cdot k$ (which corresponds to the second differential form of Gauss) we have to decide first of all what will be here the generalization of this tensor. Having particularly in mind the four-dimensional space of physics it is natural to try to consider as the generalization of the most important tensor of the theory of surfaces the most important tensor of physics and this undoubtedly is the electromagnetic tensor. At first sight there is an essential difference between these two: the tensor δ is symmetrical and the electromagnetic tensor is *anti*symmetrical; but there is a striking analogy just between the symmetrical tensor in two dimensions and the antisymmetrical in four as far as their geometrical properties are concerned: for the former there exist two perpendicular straight lines such that vectors belonging to these straight lines are transformed into vectors belonging to the same lines, this transformation being characterized by a number so that the whole tensor can be given by giving these two lines and the two corresponding numbers; for the latter there exist two (absolutely) perpendicular planes such that vectors belonging to these planes are transformed into (perpendicular) vectors belonging to the same planes, this transformation being characterized by a number so that the whole tensor can be given by giving the two planes and the two corresponding numbers.[3]

If we consider, accordingly, the electromagnetic tensor as the analogue to $s(h)$—or its representation as the analogue of the second differential form of Gauss—we may look upon the Maxwell equations as the counterparts of the Codazzi equations which must be satisfied by the coefficients of the second form (our considerations refer exclusively to the regions where *matter is absent*);[4] we can add that some results obtained by Whitta-

ker[5] permit us to say that (in a special case at least) the planes mentioned above can be considered as tangent planes to two families of surfaces just as the principal directions can be considered as tangents to the lines of curvature in the case of a surface.

If we adopt this view, viz. that the electromagnetic tensor $f(h)$ plays in the physical space the part which $s(h)$ plays on the surface we must follow that the curvature of the four-dimensional space is dependent on $f(h)$ just as the curvature of the surface depends on $s(h)$.[6] The first thing which it is natural to try as an expression of this dependence would be to take for the Riemann tensor the same expression as for the surface, viz.

$$\begin{vmatrix} f(h).x & f(k).x \\ f(h).y & f(k).y \end{vmatrix}$$

but it seems that this formula has to be slightly modified: in physics there are two nearly related tensors which have equal importance and which are sometimes referred to as the electromagnetic and the magneto-electric tensors[7] and there seems to be no reason why we should give a preference to one of them. We put therefore tentatively

$$F(x, y; h, k) = \tfrac{1}{2}\begin{vmatrix} f(h).x & f(k).x \\ f(h).y & f(k).y \end{vmatrix} - \tfrac{1}{2}\begin{vmatrix} d(h).x & d(k).x \\ d(h).y & d(k).y \end{vmatrix} \qquad (1)$$

where $d(h)$ denotes the magnetoelectric tensor (by the way, d has the same principal planes as f to which correspond the same numbers only in the inverse order). In coördinate form this tensor has to be written:

$$F_{ij,\,pq} = \tfrac{1}{2}\left\{ \begin{vmatrix} f_{ip} & f_{iq} \\ f_{jp} & f_{jq} \end{vmatrix} - \begin{vmatrix} d_{ip} & d_{iq} \\ d_{jp} & d_{jq} \end{vmatrix} \right\}. \qquad (2)$$

This tensor satisfies the algebraical conditions which are satisfied by the ordinary Riemann tensor; viz.

$$F_{ij,\,pq} = -F_{ji,\,pq};\ F_{ij,\,pq} = F_{pq,\,ij};\ F_{ij,\,pq} + F_{ip,\,qj} + F_{iq,\,jp} = 0;$$

but it does *not* satisfy the differential conditions of Bianchi:

$$F_{ij,\,pqr} + F_{ij,\,qrp} + F_{ij,\,rpq} = 0 \qquad (3)$$

which shows that the theory considered cannot be treated within the frame of the Riemann geometry based on the metrical form g_{ij}. A new representation is therefore needed and it seems that the representation introduced in the preceding paper[8] based as it is on the tensor $s(x)$ is a better starting point for this purpose.

I think it is a very strong argument in favor of the proposed expression for the Riemann tensor that if we form the contracted tensor $F_{ij} = F_{ip,\,jp}$ we obtain *exactly the energy tensor;* and it is worth while to mention that although the differential equations (3) are not satisfied the equations which we obtain from them for the contracted tensor and which seem to play an

important part in the physical theory are satisfied by F as soon as we subject f to the Maxwell equations.

[1] Cf. a note by the present writer, *Paris, C. R. Acad. Sci.*, **176**, pp. 1294–1297.

[2] These PROCEEDINGS, **9**, No. 6, June, 1923 (179–183).

[3] This will be presented in detail elsewhere.

[4] Indications as to how matter can be introduced in this theory were given in a paper read before the *Amer. Math. Soc.*; see their *Bull.*, **1923**, p. 148.

[5] *Edinburgh, Proc. R. Soc.*, **42** (1–23).

[6] Formula (11) of the paper referred to under 2.

[7] Cf. Kottler, F., *Wien. Sitz Ber. Ak. Wiss. IIa.*, **131**, pp. 119–146.

[8] These PROCEEDINGS, **9**, 1923 (401–403).

ON THE DEFORMATION OF AN n-CELL

BY J. W. ALEXANDER

DEPARTMENT OF MATHEMATICS, PRINCETON UNIVERSITY

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By an extremely simple device, Professor Veblen (These PROCEEDINGS, **3**, 1917, p. 655) has proved that every one-one continuous transformation of an n-cell and its boundary into themselves which leaves invariant all points of the boundary may be realized by a deformation. However, the deformation is of such a character that the boundary of the n-cell does not remain invariant but merely returns to its initial position as the deformation is completed. A slight modification of Professor Veblen's scheme gives a deformation during the entire course of which the boundary remains pointwise invariant. I shall give the proof only for the case $n = 2$, since the generalization to higher dimensions is immediate.

Let the 2-cell and its boundary be represented by the interior and periphery of the unit circle C_1. Any one-one continuous transformation T of the 2-cell into itself may then be expressed by a pair of equations in polar coördinates of the following form:

$$r^1 = R(r, \varphi), \qquad \varphi^1 = \Theta(r, \varphi), \tag{T}$$

where R and Θ are defined within the unit circle. Moreover, if the transformation is pointwise invariant on the boundary C_1 of the 2-cell, we must also have

$$R(1, \varphi) = 1, \qquad \Theta(1, \varphi) = \varphi.$$

We shall extend the region of definition of the transformation T over the entire plane by putting

$$R(r, \varphi) = r, \Theta(r, \varphi) = \varphi, \text{ for } (r \geqq 1).$$

Clearly, then, the extended transformation will leave invariant all points on or without the unit circle C_1.

Now, consider the family of transformations

$$r^1 = \lambda R(r/\lambda, \varphi), \qquad \varphi^1 = \Theta(r/\lambda, \varphi), \qquad (1 \geq \lambda > 0) \qquad (T_\lambda)$$

where λ is a parameter. Evidently, the transformation T_λ leaves invariant all points on or without a circle C_λ of radius λ with centre at the origin, and determines within the circle C_λ a transformation which is merely a replica on a different scale of the transformation determined by T within the unit circle C_1. Thus, as λ approaches zero, the transformation T_λ merges continuously into the identity, which makes it reasonable to define T_0 as the identity. For $\lambda = 1$, the transformation T_λ reduces to T.

The desired deformation is the one determined by T_λ as λ increases continuously from 0 to 1. Evidently, the unit circle remains invariant during the deformation, since it is never interior to the circle C_λ.

The above theorem was proved for the case $n = 2$ by H. Tietze (*Palermo, Rend., Circ. Mat.*, **38**, 1914, pp. 247–304) and, more simply, by H. L. Smith (*Annals Math.*, **19**, 1918–19, pp. 137–141). The present proof, however, generalizes at once to n dimensions, as has already been remarked.

CONTROL OF THE APPEARANCE OF PUPA-LARVAE IN PAEDOGENETIC DIPTERA

BY REGINALD G. HARRIS

BROWN UNIVERSITY

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It has been known for some time (Wagner 1861) that Miastor reproduces during much of its life-cycle by paedogenesis. Ordinarily this mode of reproduction maintains throughout the autumn, winter and spring, until early summer when pupae occur, giving rise to male and female imagines. With these two modes of reproduction occurring, viz. paedogenesis and normal adult sexual reproduction, it is natural that there should be polymorphism among the larvae of Miastor,[1] one type reproducing by paedogenesis and incapable of metamorphosing into pupae, the other type giving rise to pupae but incapable of paedogenesis.

It seemed desirable to ascertain, if possible, what factors control the appearance of the different types, the more so as I had observed, in one instance, pupa-larvae and pupae occurring in nature together with paedo-

genetic larvae in October. With this in view the present studies were undertaken.

The colony, just mentioned, was found in a decaying birch log at Hill 108, Berry au Bac, France, under the following conditions. The log, which was apparently part of a dugout used during the war, was lying at the bottom of a mine crater. The hill, having been mined on several occasions, and having been the object of much shell fire, was extremely desolate, free from vegetation save for a few weeds, while the crater itself was an absolute desert. There were no other logs in the immediate vicinity. The members of the colony were extremely numerous, and lay in close contact with one another forming compact masses.

The material was taken to the laboratory where many larvae were removed, together with small pieces of wood, from the log, and placed in a covered tin box at room temperature. In this material paedogenetic larvae were by far the most numerous type until late in December when many of the larvae were observed to be pupa-larvae. In early January it was extremely difficult to find paedogenetic larvae in the material. On the other hand in the (original) log, which was placed in the cellar under as nearly natural conditions as practicable, and from which several hundred larvae had been removed, pupa-larvae became less numerous until finally none were observed.

This striking difference in the type of offspring of larvae, chosen in large numbers at random from a single colony, one group of larvae now being predominantly paedogenetic, while the other group was not, seemed to indicate that the factors inducing polymorphism in Miastor, at least in so far as paedogenetic and pupa-larval forms are concerned, are external.

In both cases in which pupa-larvae were observed, viz. in the log at Berry au Bac and in the tin box in the laboratory, the coincidence of one condition seemed striking: theoretically unlimited means of increase in the number of individuals in the colony by paedogenesis, with an obvious limit to the extent of suitable habitat available for the members of the colony; this limit being imposed at Berry au Bac by the lack of other logs, and in the laboratory by the limits of the tin box.

Previously Springer[2] had observed pupae occurring in the laboratory in the winter. He loosened the bark of a log in which he had found Miaster larvae, otherwise maintaining the colony under as natural conditions as practicable. He arrived at the conclusion, in the absence of stated controls, that the appearance of pupa-larvae is induced by the action of light upon paedogenetic mothers, since he believed that the other environmental conditions of the colony were natural.

Springer's explanation, in view of the fact that I had found pupa-larvae occurring in nature underneath the opaque bark of a birch log, did not seem satisfactory.

A series of experiments conducted in France[3] on *Miastor metraloas* Meinert further indicated that light is not the influencing factor in the production of pupa-larvae.

Recently-born broods from isolated mothers were separated into two groups of cultures, one being exposed to light, the other kept in darkness. The cultures were followed through two generations, at the end of which no pupa-larvae were observed in either group. Though the experiments seemed clearly to indicate that light alone does not induce the appearance of pupa-larvae, they were not completely conclusive as they were conducted before a wholly satisfactory technique of artificial culture had been found, and the number of surviving larvae at the end of the second generation was not great.

Recently a series of experiments has been concluded at the Biological Laboratory at Cold Spring Harbor,[4] on material[5] collected in the vicinity of the laboratory, which clearly demonstrates the non-effectiveness of light as a factor in the production of pupa-larvae. A series of cultures was arranged, half of the cultures being exposed to light, the other half left unexposed. Eight paedogenetic larvae, doubtless sisters and cousins, and consequently theoretically similar, having arisen parthenogenetically in the same colony, were placed in each Petri dish, all environmental factors, save light, presumably being alike in cultures of a given series, though temperature varied in different series. The cultures exposed to light and the controls were placed in incubators at the desired temperature. Cultures exposed to light were placed between two 16 candle-power electric lights, each light being 9 inches distant from the Petri dish, and on the same level with it. Controls were placed in a covered box, which was in turn put within another covered box, and were maintained on the same shelf in the incubator with the exposed culture of its series.

The following table will give the results of these experiments. Section

TABLE I

RESULTS OF AN EXPERIMENT TO ASCERTAIN THE RÔLE OF LIGHT VIS A VIS WITH THE APPEARANCE OF PUPA-LARVAE

		B_{11}	B_{12}	C_{11}	C_{12}
A	Paedogenetic larvae	5	36	15	22
	Pupa-larvae or pupae	0	0	7	7
	Undetermined	0	31	0	0
	Total number of larvae	5	67	22	29
B	Paedogenetic larvae	3	9	3	11
	Pupa-larvae or pupae	0	11	7	7
	Undetermined	0	45	0	11
	Total number of individuals	3	65	10	29
C	Paedogenetic larvae	6	2		3
	Pupa-larvae or pupae	1	38	Discon-	27
	Undetermined	0	21	tinued	26
	Total number of individuals	7	61		56

It is possible that some of the larvae listed in sections A and B as paedogenetic larvae may have been young pupa-larvae as methods of recognizing pupa-larvae, other than by the presence of the spathula sternalis, are not practicable in examining larvae within a Petri dish. The spathula sternalis not being visible in young pupa-larvae, it sometimes happens that young pupa-larvae pass for paedogenetic larvae when examined in agar.

Undetermined larvae are those which by their position in the Petri dish, usually at regions of curvature in the glass, cannot be examined under the microscope. There is every reason to believe that many, if not all, the undetermined larvae in section C are pupa-larvae.

Pupa-larvae have also arisen in a culture maintained at unheated room temperature; i.e., a temperature similar to that occuring in nature during this season (September). In this culture 19 individuals were originally present, but this number was gradually reduced, presumably by the lethal effect of light, until 4 weeks after starting the culture only 3 individuals were present, of these 2 are pupa-larvae, 1 is a resting mother, paedogenetic larva.

A contains countings made two weeks after the experiment was commenced, section B three days later, and section C one week after section B. In each culture 8 larvae, all paedogenetic, were originally present. No pupa-larvae were found in the original colony from which the material was taken though several hundred larvae have been examined. B cultures were placed in an incubator at 23° C., C cultures at 28° C. Odd numbered cultures were exposed to light, even numbers unexposed, save in the case of B_{11} which was placed in darkness after the counts in section B had been made, and remained unexposed to light for a week before the counts in section C were made. Other cultures (A) were maintained at unheated room temperature. These will be discussed later.

Several facts are suggested by the foregoing table. 1st. Light is not an activating factor in the production of pupa-larvae. It will be noted that during the first two weeks (section A) in cultures at a temperature of 28° C. pupa-larvae occurred in fairly equal proportions whether the culture were exposed to the influence of light or whether it remained unexposed. During the first 17 days (sections A & B) in cultures at 23° C. in the culture exposed to light no pupa-larvae occurred, while in the culture which remained unexposed pupa-larvae early occurred in a fairly large proportion, which steadily increased until nearly all were pupa-larvae.

A difference of temperature of from 23° C. to 28° C. does not seem to have a noticeable effect in the production of pupa-larvae, save that pupa-larvae appeared earlier in the culture at 28° C., due no doubt to increased speed of reproduction at the higher temperature. In fact with the eventual appearance of pupa-larvae in a culture maintained at unheated room temperature during September it seems safe to conclude that temperatue, like light, is not an activating factor in inducing the appearance of pupa-larvae, though at a lower temperature, as would be expected, the arising of new generations being greatly retarded, the appearance of pupa-larvae is similarly retarded.

These experiments further demonstrate a fact, which I have already observed in experimenting with *Miastor metraloas*, viz. that light has a slowly acting lethal effect especially on paedogenetic larvae.

The only culture at a temperature of either 23° or 28° C. in which pupa-larvae did not arise during the first 17 days, was a culture, B_{11} at 23° C., in which there was a small number of individuals, the number having been reduced from 8 to 5 and later to 3, presumably by the slowly acting lethal effect of exposure to light. A similar reduction occurred in culture C_{11} at 28° C. Here, apparently, however, the greater speed of reproduction, due to higher temperature, permitted a temporary increase in the number of individuals, from 8 to 22, before the lethal effect of light had had sufficient time to operate. In this culture pupa-larvae occurred when the individuals were most numerous.

After 17 days exposure to light culture B_{11} was placed in the dark where it remained for seven days. At the end of this period the number of larvae had increased from 3 to 7, one of the 7 being a pupa-larva (section C). Section C is further very significant in view of the large increase over the counts of sections A & B in the number of pupae and pupa-larvae which are present. The data would seem to indicate that whatever the conditions which bring about the appearance of pupa-larvae, they are becoming more imperious as the cultures continue, especially if the number of larvae increases.

There seems to be here, as well as in the material found at Berry au Bac and in that maintained in the tin box in the laboratory at Paris, some indication that pupa-larvae arise under crowded conditions and in old cultures presumably containing an unusually large amount of the bi-products of metabolism. It is possible that other factors may also be influential in inducing the appearance of pupa-larvae. There seems to be little doubt, however, but that these factors are external.

Other facts of interest have been brought to light as a result of continued observation. It has been found that, contrary to previous belief, the pupa is not formed within the last larval skin, at least in the American species under observation at the present time, but that moulting occurs between the larval and pupal stages.

In this study light has been thrown upon the function of the spathula sternalis, a structure typical of Cecidomyid larvae, but occurring only in pupa-larvae, being absent in paedogenetic types. Many possible functions have been suggested. "By some it is thought to be a pseudopod; by others a mentum; and Miss Ormerod believes its function is that of a scraper or digger in obtaining food from stems. More probably its use is for locomotion, or for changing the position of the larvae in its cocoon or case."[6]

I have observed that in the moulting previous to the metamorphosis from the larval to the pupal stage the spathula sternalis is left behind with

the last larval skin. Obviously the spathula sternalis can be of no service to the pupa in this species. In some cases the larva emerged by pushing the spathula sternalis outward, tearing it free for the most part from the surrounding tissue, thus making an exit. I am not certain that this always occurs. The fact that the spathula sternalis does not occur in paedogenetic Cecidomyid larvae would seem to indicate, however, that it is not essential for locomotion or feeding, and suggests that it might be connected with some phase, distinctive to pupa-larvae, viz. moulting. It is possible that the function of the spathula sternalis in this species is somewhat similar to that of the "anchor-shaped egg burster" of certain Hemiptera (Podops cinctipes Say).[7] It is interesting to note in this connection that the spathula sternalis is called the "anchor-process" in England.

Within the past few weeks, after consulting with Dr. A. F. Blakeslee, an advance has been made in standardizing and simplifying the culture medium until now the following medium is being employed with very satisfactory results. Malt extract 0.5%, agar agar 2.5%, water 97%. The medium is prepared in the usual manner of preparing agar media. It should be filtered before sterilization in order to render it fairly transparent, thus permitting examination of individuals of a culture in the Petri dish without difficult manipulation. Yeast is not added to the medium, larvae being permitted to innoculate the culture with the microörganisms among which they occur in nature. Good results are obtained with this medium at a temperature of from 22° C. to 28° C. The culture should not be exposed to light for long periods of time. The presence of beef extract in medium is harmful to the normal development of the colony.

In conclusion, these experiments would seem to indicate that pupa-larva arise in the laboratory under conditions which are unfavorable to continued paedogenetic reproduction. Of the external conditions which might be factors in inducing the appearance of pupa-larvae light and constant temperature of different degrees have been found to exert no influence, save in so far as the former tends to kill paedogenetic larvae, thereby increasing the proportion of pupa-larvae in cultures which still contain paedogenetic larvae, and in so far as the latter hastens or retards the appearance of pupa-larvae by hastening or retarding the appearance of daughter generations.

Since pupa-larvae occurred either in old or crowded cultures, at high or low temperature, whether exposed to light or not, the old cultures in these cases having once been crowded, there would seem to be some indication that the conditions which induce the appearance of pupa-larvae at the expense of continued paedogenetic reproduction in Cecidomyidae are concurrent with or subsequent to (i.e., accumulation of bi-products) crowding. Experiments are being carried on in an attempt to ascertain what the factors are.

[1] For description of polymorphism in Miastor see Harris, R. G., "Occurrence, Life-cycle, and Maintenance under Artificial Conditions of Miastor." *Psyche*, **30**, pp. 79 (1923).

[2] Springer, Fritz. "Polymorphismus bei den Larven von *Miastor metraloas*." *Zool. Jahrb. Abth. J. Anst.*, **40**, p. 57 (1917).

[3] At the Laboratoire de l'évolution des êtres organisés, Paris. Prof. M. Caullery, Director.

[4] Acknowledgment is made to Dr. C. B. Davenport for facilities and suggestions offered in connection with this work at the Dept. of Genetics of the Carnegie Institution of Washington at Cold Spring Harbor.

[5] Oligarces, closely related to Miastor and having a similar life-cycle. A description of the species will appear shortly.

[6] Williston, S. W., *North American Diptera*, 3rd. Edit., p. 120.

[7] Parshley, H. M., *The Canadian Entomologist*, **55**, pp. 69–70.

THE WAVE-LENGTHS OF SECONDARY X-RAYS

BY GEORGE L. CLARK AND WILLIAM DUANE

JEFFERSON PHYSICAL LABORATORY, HARVARD UNIVERSITY

Communicated October 30, 1923

Some years ago, researches on the spectra of secondary X-rays were begun in our laboratory. The object of these researches was to measure accurately with a spectrometer the fluorescent spectra of chemical elements, the idea being: (*a*) to find out whether any appreciable difference in wave-length exists between the lines in the fluorescent spectra and those in the emission spectra obtained in the usual way with the elements in the target of the X-ray tube, and (*b*) to determine the wave-lengths of the lines in the spectra of the elements, which have not yet been recorded.

Previously Duane and Shimizu[1] had measured by means of a spectrometer the wave-lengths of fluorescent X-rays belonging to the α and β lines in the L series of lead.

Recently the work has been taken up again with greatly improved apparatus. During the course of these researches, phenomena appeared from which the wave-lengths of the scattered radiation coming from the secondary radiator can be determined, and the object of this preliminary note is partly to present data which bear upon the important question under discussion at the present time, namely, whether any differences exist between the wave-lengths of scattered X-rays and those of the primary rays that produce them.

In our experiments we used a Coolidge tube with a tungsten target. A current of about two milliamperes passed through the tube coming from a generating plant (previously described) consisting of transformers,

kenotrons and electrical condensers so arranged as to produce a constant non-fluctuating voltage of 80,000 to 90,000 volts. This voltage suffices to produce fairly intense lines in the K series of the tungsten target, which have wave-lengths in the neighborhood of .2 ångström.

Figure 1 represents the arrangement of the apparatus. The primary X-rays come from the target of the X-ray tube and fall upon the secondary radiator which lies opposite a slit, 1, between lead blocks. Some of the secondary rays from the radiator pass through slit 1, a hole in the brick wall and a second slit, 2. A large lead screen, $^3/_8$ inch thick, fastened against the wall, as indicated, gives additional protection to the X-ray spectrometer which lies in a room adjoining that containing the X-ray tube and the generating plant. The rays from the secondary radiator, after passing through slits 1 and 2, strike the calcite crystal of the spectrometer which reflects some of them into the ionization chamber. A sensitive quadrant electrometer measures the ionization current in the usual way. A thick sheet of lead lies between the tube and the first slit $S1$ and prevents the primary X-rays from striking the sides of this slit. We found by experiments that this protection was very important, for, without it, our spectrometer readings indicated radiation that did not come from the radiator itself, and that might have been interpreted as evidence of scattered radiation from the radiator having a wave-length differing from its true value.

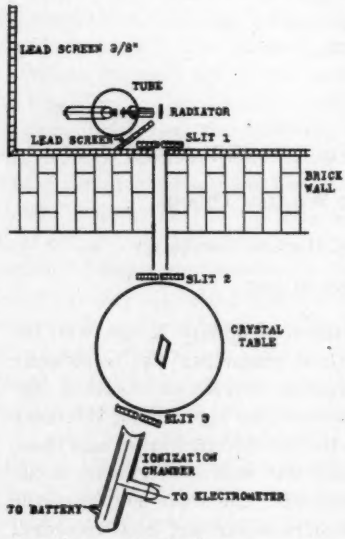

FIGURE 1

The curves in figures 2 and 3 represent the ionization currents as functions of the positions of the crystal, the ionization chamber always being placed in such a position as to receive the reflected beam. In the experiments represented by figure 2 the secondary radiator consisted of a barium salt (barium chloride) and in those represented by figure 3 the secondary radiator consisted of a lanthanum salt (lanthanum oxide). The curves correspond to readings taken on both sides of the zero line of the spectrometer, and the angle θ, to be substituted in the Bragg equation for the wave-length, λ, namely $n\lambda = 2d \sin \theta$, is $^1/_2$ the angle measured from a point on the curve to the corresponding point on the curve on the other side of the zero line.

A number of peaks occur on the curves. Some of the peaks (as indicated in the figures) correspond to the Kα and Kβ lines of the tungsten target reflected in the spectra of the first and second orders. The other peaks correspond to the K lines of the chemical elements in the secondary radiator, barium or lanthanum as the case may be.

Table 1 contains the readings of the vernier that determine the angular positions of the crystal corresponding to the various peaks, beginning with the peaks nearest the zero line of the spectrometer.

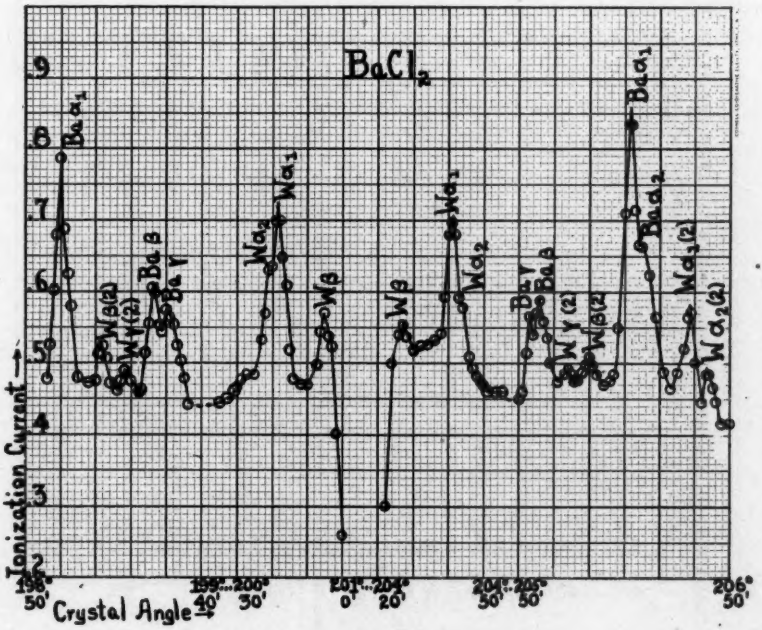

FIGURE 2

Table 2 contains the wave-lengths corresponding to the various peaks as calculated from the Bragg equation. The wave-lengths of the scattered rays were calculated from the second order spectra, where the α_1 line appears completely separated from the α_2 and the β from the γ. The numbers in parentheses are the recorded wave-lengths of the various lines in the primary spectra obtained with the corresponding chemical elements in the target of the X-ray tube. The wave-lengths for tungsten were measured in our laboratory,[2] and those for the other chemical elements in Siegbahn's.[2] The table also contains the wave-lengths corresponding to peaks determined in experiments similar to those for barium and lan-

TABLE I

ANGULAR POSITIONS OF CRYSTAL CORRESPONDING TO VARIOUS PEAKS

CHEMICAL ELEMENT	SPECTRUM LINE	SPECTRUM ORDER	BARIUM RIGHT	BARIUM LEFT	CHEMICAL ELEMENT	SPECTRUM LINE	SPECTRUM ORDER	LANTHANUM RIGHT	LANTHANUM LEFT
Tungsten	β	1	204°26′	200°55′	Tungsten	β	1	204°25′	200°56′
Tungsten	α_1	1	204°40′1/2	200°41′1/2	Tungsten	α_1	1	204°39′	200°42′
Tungsten	α_2	1	204°43′1/4	200°39′	Tungsten	α_2	1	204°41′1/2	200°39′
Barium	γ	1	205°52′	199°30′1/2	Lanthanum	γ	1	205°45′	199°42′
Barium	β	1	205°56′	199°26′1/2	Lanthanum	β	1	205°49′	199°39′
Tungsten	γ	2	206° 4′	199°18′	Tungsten	γ	2	206° 5′	199°17′1/2
Tungsten	β	2	206°10′	199°12′	Tungsten	β	2	206°11′	199°12′
Barium	α_1	1	206°21′1/2	199°00′	Lanthanum	α_1	1	206°13′1/4	199° 9′
Barium	α_2	1	206°25′		Lanthanum	α_2	1	206°15′1/2	199° 7′1/2
Tungsten	α_1	2	206°38′1/2		Tungsten	α_1	2	206°39′1/4	198°43′1/4
Tungsten	α_2	2	206°43′1/2		Tungsten	α_2	2	206°44′1/4	198°38′1/4

TABLE II

WAVE-LENGTHS CALCULATED FROM POSITIONS OF PEAKS ON IONIZATION CURVES

SECONDARY RADIATORS	FLUORESCENT WAVE-LENGTHS α_2	α_1	β	γ	SCATTERED WAVE-LENGTHS α_2	β	γ
Potassium Iodide	.4417	.4368	.3878	.3818	.2130	.2086	.1842	.1789
	(.——)	(.437)	(.388)	(.—)				
Barium Chloride	.3943	.3886	.3429	.3359	.2134	.2090	.1840	.1787
	(.393)	(>.388)	(.343)	(.—)				
Lanthanum Oxide	.3767	.3735	.3257	.3196	.2140	.2086	.1844	.1794
	(.376)	(.372)	(.329)	(.—)				
Praseodymium	.3486	.3433	.3011	.2958	.2130	.2086	.1840	.1796
	(.347)	(.342)	(.301)	(.—)				
Neodymium Carbonate	.3345	.3301	.2923	.2871				
	(.—)	(.330)	(.292)	(.—)				
					PRIMARY WAVE-LENGTHS			
					(.2134)	(.2086)	(.1842)	(.1790)

thanum in which the secondary radiators consisted of potassium iodide, neodymium carbonate and praseodymium carbonate, respectively.

It appears from the table that the wave-lengths of the fluorescent rays coming from the chemical elements employed as secondary radiators do not differ from those obtained when the elements are used in a target by more than a small fraction of 1%, which is no larger than the errors of measurement in experiments of this kind. In other words, the wave-lengths of lines in the secondary fluorescent spectrum of a chemical element equal, within the experimental errors, the wave-lengths of the same lines excited by the bombardment of the same chemical element by electrons in an X-ray tube. This agrees with the modern theory of X-radiation.

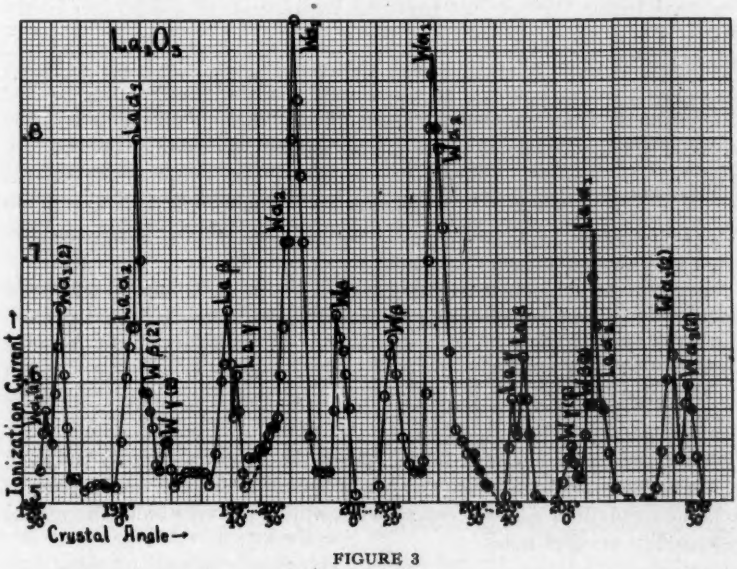

FIGURE 3

The frequencies of the fluorescent lines, to a remarkable degree of accuracy, equal the differences between critical absorption frequencies (where these have been recorded), as they should according to the combination principle; and the square roots of these frequencies are nearly linear functions of the atomic numbers of the chemical elements.

An examination of the heights of the peaks shows that the relative intensities of the lines in the K series of fluorescent rays are substantially the same as the relative intensities recorded for the primary rays from tungsten, molybdenum and rhodium.

Further, the peaks representing scattered X-rays from the K series lines of the tungsten target correspond to wave-lengths that are precisely

equal to those measured in the primary radiation coming directly from the tungsten target itself. In other words, secondary radiation contains a large number of scattered rays of precisely the same wave-lengths as those of the primary rays.

We have not been able to detect the presence of any rays in the secondary radiation having wave-lengths a certain fraction of an ångström longer than those of the primary rays, as an interesting theory recently published by A. H. Compton[3] demands. According to this theory, the scattered rays at right angles to the primary beam ought to have wave-lengths .024 ångström longer than those of the primary rays and this difference should be independent of the wave-lengths of the primary, exciting rays. The wave-length shift of .024 ångström corresponds to a difference in the setting of our reflecting crystal of about 13′ or 14′. There are no peaks on our curves 13′ or so further away from the zero line than the tall peaks corresponding exactly with the wave-lengths of the strong α lines in the K series of the tungsten target. Undoubtedly, there are some rays in the secondary radiation having wave-lengths longer than those of the primary rays, but the amount of this radiation having the definite wave-lengths shift .024 appears from our experiments to be inappreciable as compared with the amount of scattered radiation having wave-lengths precisely equal to those of the primary rays.

In some very important experiments (*l. c.*), A. H. Compton showed a definite difference in wave-length between the primary and scattered radiation when he used the K series lines of molybdenum as the primary radiation. The molybdenum lines have wave-lengths in the neighborhood of .7 ångström, i.e., $3^1/_2$ times as long as the tungsten lines. In these experiments he employed carbon as the secondary radiator. We have, therefore, repeated our experiments using the K series lines of tungsten as the primary radiation with carbon, aluminium, sulphur and copper as secondary radiators. These experiments will be described and the results discussed in another note.

[1] *Physic Rev., Ithaca*, Nov. 1919, 391.

[2] See *Bull. Natl. Res. Council, Washington*, Nov. 1920.

[3] *Bull. Natl. Res. Council*, Oct. 1922, p. 16; *Physic. Rev.*, May 1923, p. 483 and June 1923, p. 715.

THE WAVE-LENGTHS OF SECONDARY X-RAYS (*Second note*)

BY GEORGE L. CLARK AND WILLIAM DUANE

JEFFERSON PHYSICAL LABORATORY, HARVARD UNIVERSITY

Communicated Oct. 31, 1923

In a previous note[1] the authors have described experiments on the wave-lengths of secondary X-rays produced in secondary radiators, consisting of potassium iodide, barium chloride, lanthanum oxide, praseodymium carbonate and neodymium carbonate. The researches showed that, within the errors of experiment, the wave-lengths of the secondary fluorescent X-rays have the same values as those of the characteristic K series lines of the X-ray spectra when potassium, barium, lanthanum praseodymium and neodymium, respectively, are used in the targets of the X-ray tube. In other words, the lines in the characteristic spectrum of a chemical element have the same wave-lengths, whether they are excited by the bombardment of electrons or by primary X-rays. It appeared also that the relative intensities of the lines of the K series were substantially the same in the two cases. Further, the experiments indicated that a large amount of the secondary radiation (scattered rays) has the same wave-lengths as the primary rays in the K series of X-rays characteristic of the tungsten target. We obtained no evidence of radiation comparable in intensity with this scattered radiation and having wave-lengths .024 ångström longer than the primary wave-lengths, as an interesting theory of Prof. A. H. Compton's[2] demands.

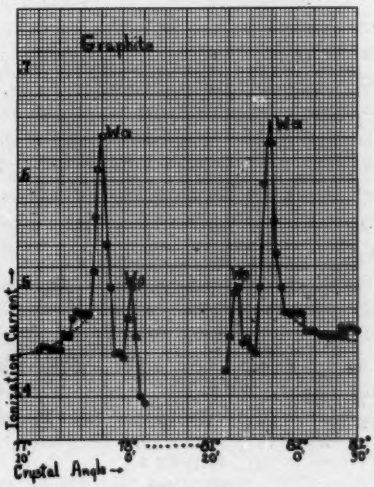

FIGURE 1

In our experiments we employed the X-rays from a tungsten target as the primary, exciting X-rays. Professor Compton[2] has published accounts of important experiments in which he used the rays from a molybdenum target. His experiments indicate the presence of scattered radiation having wave-lengths averaging .024 ångström longer than the primary rays, when carbon was used as a secondary radiator. The radiation was analyzed by means of an ionization spectrometer. More recently, P. A. Ross[3] has published the results of experiments by the photographic method

and with a molybdenum target, which appear to confirm the wave-length shift observed by Compton. The shifted wave-lengths, however, occupy a band in the spectrum that is broad as compared with the primary.

We have repeated our experiments using as secondary radiators chemical elements of lower atomic weight than those mentioned above, namely, carbon, aluminium, sulphur and copper. The primary, exciting radiation was, as before, the X-rays from a Coolidge tube with a tungsten target operated at a constant voltage of eighty to ninety thousand volts, and including, therefore, the K series lines of tungsten. The tungsten K lines have wave-lengths in the neighborhood of .2 ångström, whereas those of molybdenum lie in the neighborhood of .7 ångström.

The exact arrangement of the apparatus is represented in figure 1 of the previous note. We have made four experiments with graphite as the secondary radiator. The curve in figure 1 of this note represents the results of one of these experiments. The abscissas of the two curves give the angular positions of the crystal corresponding to reflections of X-rays on the two sides of the zero line of the spectrometer, the ordinates are the corresponding ionization currents. The tall peaks represent the α and β lines in the K series of tungsten and correspond to the wave-lengths of these tungsten lines, the wave-lengths being calculated by the Bragg formula using half the angular distance between corresponding peaks. The curves indicate a large amount of scattered radiation having precisely the wave-lengths of the primary radiation exciting it.

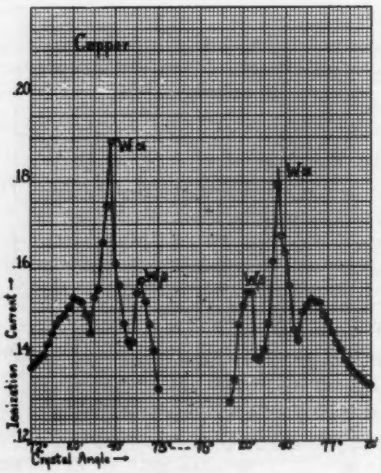

FIGURE 2

The secondary rays come from the radiator at right angles to the primary rays and Compton's theory demands that in this case the shift in the scattered radiation should amount to .024 ångström and should be independent of the wave-lengths of the primary, exciting rays. This wave-length shift of .024 corresponds to between thirteen and fourteen minutes of arc on the scale giving the position of our calcite crystal. It appears from the curve that there is no especially large amount of radiation corresponding to points thirteen or fourteen minutes away from the α peaks themselves. The latter correspond with the wave-lengths of the primary tungsten spectrum to within the errors of measurement. In

other words, in the case of tungsten primary radiation there is no evidence for scattered rays, having wave-lengths exactly .024 ångström longer than the primary rays, and with an intensity at all comparable with the scattered rays of precisely the same wave-lengths as the primary.

In this particular curve there are small irregularities thirteen or fourteen minutes from the α peaks. We have chosen this curve for representation because it is the only carbon curve which does show such irregularities. If we took an average of our four experiments with carbon, the curve would run about as represented by the dotted line, which also indicates no especially strong radiation thirteen or fourteen minutes from the α peaks.

Our experiments with aluminium and sulphur have lead to the same results. We found markedly intense radiation at wave-lengths within experimental errors, equal to those of the α and β lines in the K series of the tungsten target but no evidence of any especially intense lines having wave-lengths 0.24 ångström longer.

The curves in figure 2 represent secondary radiation from a plate of copper. These curves also have tall peaks that correspond to wave-lengths equal to those of the α and β lines in the K series of the tungsten target. In addition to these, there is evidence of an excess of radiation represented by the two humps on the outside of the X-peaks at a distance of seventeen or eighteen minutes from the X-peaks. It is difficult to estimate just how much radiation these humps indicate for part of them at least may be due to the form of the continuous spectrum radiation curve. The continuous spectrum radiation curve always has a maximum, the position of which depends upon the voltage applied to the tube and the amount of matter that the X-rays have passed through, etc. The distance of the humps on the copper curve from the α-peaks is somewhat greater than the maximum distance demanded by Compton's theory.

The following table contains the wave-lengths corresponding to the peaks on our ionization curves, the values being calculated from the Bragg formula.

WAVE-LENGTHS OF SCATTERED X-RAYS (In ångströms)

SCATTERING SUBSTANCE	GRAPHITE	GRAPHITE	GRAPHITE	GRAPHITE	ALUMINIUM
α Lines	.2100	.2098	.2098	.2104	.2098
β Lines	.1841	.1858	.1851	.1850	.1845
SCATTERING SUBSTANCE	SULPHUR	SULPHUR	COPPER	AVERAGE VALUES	
α Lines	.2105	.2096	.2098	α .2100	
β Lines	.1878	.1850	.1854	β .1850	
Primary Rays Direct from Target		α_2 = .2134, α_1 = .2086, β = .1841			

It appears that the wave-lengths of the rays scattered from the $K\alpha$ doublet of the tungsten target lie between that of the strong α_1 line and that of the weaker α_2 line and nearer the former. Further, the values of the wave-lengths of the rays scattered from the β group are on the average

a fraction of one per cent larger than that of the primary X-rays. This difference does not appear to be greater than experimental errors in this case, for the β peaks lie on portions of the general radiation curves that are rapidly rising, and we would expect from this a slight apparent shift toward longer wave-lengths.

Undoubtedly among the secondary X-rays there is a certain amount of radiation having longer wave-lengths than the primary, exciting rays. Our experiments with copper, however, are the only ones in which we have found evidence of radiation with wave-lengths longer than the primary by a definite amount.

The transfer of energy and momentum from a quantum of radiant energy to a single, free electron forms the basis of Compton's theory of scattered radiation. Another line of thought indicates that there must be tertiary rays having wave-lengths longer than the primary rays by a certain amount. The fundamental idea of this is that the photoelectrons produced by the primary rays, when they strike neighboring atoms, must produce radiation just as the electrons in the X-ray tube produce it, when they strike the atoms of the target. Mr. Hu[4] showed in his doctor's thesis that the energy of the photoelectrons due to X-rays was a few per-cent less than the $h\nu$ value of the primary radiation. De Broglie[5] has published accounts of important investigations, which show that the difference between the energy of the photoelectrons and the $h\nu$ value of the incident radiation equals the energy required to lift an electron completely out of the atom. This latter energy equals the $h\nu$ value of the critical absorption frequency of the chemical element from which the photoelectrons come. When electrons strike ordinary atoms they produce continuous spectrum radiation having a short wave-length limit, the $h\nu$ value of which equals their kinetic energy. We would, therefore, expect the photoelectrons due to X-radiation to produce a tertiary radiation of lower frequency and, therefore, of longer wave-length than the primary. The short wave-length limit of this tertiary radiation ought to be a definite amount longer than the wave-length of the primary rays, this amount depending upon the chemical element used as a secondary radiator.

If ν_1 and ν_2 represent the frequency of the primary radiation and the critical absorption frequency of the secondary radiator, respectively, then the frequency, ν, of the limit of the tertiary radiation may be calculated from the equation.

$$h\nu = h\nu_1 - h\nu_2.$$

The frequency shift of the limit of the tertiary radiation from the primary is

$$\nu_1 - \nu = \nu_2.$$

For any particular chemical element, used as a secondary radiator, ν_2 is

constant and the frequency shift for such an element is independent of the wave-lengths of the primary rays. In Compton's theory the wave-length shift turns out to be independent of the primary wave-lengths.

Calculating the wave-length of the limit of the tertiary radiation in terms of the wave-lengths λ_1 and λ_2 we have

$$\lambda = \frac{\lambda_1\lambda_2}{\lambda_2-\lambda_1},$$

and for the wave-length shift

$$\lambda - \lambda_1 = \frac{\lambda_1^2}{\lambda_2-\lambda_1}.$$

If the critical absorption wave-length, λ_2, is large compared with the primary wave-length, λ_1, the wave-length shift becomes approximately proportional to the square of the primary wave-length. In our experiments with sulphur and aluminium $\lambda_2 = 5.0$ and 7.9, respectively, and $\lambda_1 = .21$. Hence the wave-length shifts amount to only about .009 and .006, respectively, and the limits of the tertiary spectra lie so close to the α and β lines that they would not be appreciable on our curves. In the experiment with carbon the limit of the tertiary spectrum would lie still closer to lines in the primary radiation.

If the secondary radiator consists of copper the limit of the tertiary radiation lies some distance from the lines in the primary rays. For copper $\lambda_2 = 1.38$ and the tertiary radiation due to the photoelectrons ought to have a short wave-length limit .037 ångström longer than the wave-length of the primary K line. This difference in wave-length corresponds to about 20 minutes of arc in the position of the calcite crystal in our experiments. Hence, we would expect to find some radiation of wave-lengths roughly corresponding to the humps actually observed on our copper curves.

Applying this theory to the experiments by Compton and those by Ross, we find the following estimate of the shift in the wave-length of the tertiary radiation. The K critical absorption wave-length of carbon has been estimated from ionization potentials and found to be in the neighborhood of 42 ångström (Foote and Mohler). Calculating from this the shift in wave-length if we use the Kα line of molybdenum as primary radiation, we find that it should be of the order of magnitude of .012 ångström. According to our theory, therefore, there ought to be tertiary radiation beginning at a wave-length something like .012 ångström longer than the Kα line of molybdenum, and having an average wave-length somewhat longer still. Just how much longer we do not know for the position of the maximum of the general radiation depends upon a great variety of experimental conditions. The position of the maximum for instance ought to depend somewhat on the angle of incidence of the primary X-rays. Possibly the radiation observed by Compton and Ross

may be the peak of this continuous spectrum radiation due to the bombardment of the photoelectrons against neighboring atoms in the secondary radiator. This theory would explain for instance the fact that the observed radiation is a band much broader than the lines of the primary rays.

[1] These PROCEEDINGS, Dec. 1923.

[2] *Bull. Natl. Res. Council*, Oct. 1922, p. 16: *Physic. Rev.*, May 1923, p. 483, and June 1923, p. 715.

[3] These PROCEEDINGS, July 1923, p. 246.

[4] *Physic. Rev.*, June 1918, p. 505.

[5] *Comptes Rendus, Paris*, Jan. 31: March 29: Sept. 26, 1921; *J. Physique*, Sept. 1921.

SYMBIOSIS BETWEEN TERMITES AND THEIR INTESTINAL PROTOZOA[1]

BY L. R. CLEVELAND

DEPARTMENT OF MEDICAL ZOÖLOGY, SCHOOL OF HYGIENE AND PUBLIC HEALTH, JOHNS HOPKINS UNIVERSITY

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A correlation between the presence of intestinal protozoa in termites and a wood-feeding habit was postulated by Imms,[2] and this, if true, as Imms pointed out, indicates a possible symbiotic relationship between termites and their intestinal protozoa. After making several microchemical tests on the protozoa, Buscalioni and Comes[3] concluded that the protozoa digest the wood particles which they take into their bodies; and from this conclusion, without stopping to consider whether or not the protozoa can digest wood, these authors claim that they have established symbiosis between termites and their intestinal protozoa. Other investigators, notably Grassi[4,5] and Kofoid,[6] though devoting most of their time to systematics and morphology, have usually regarded the protozoa either as commensals or parasites. Recent investigations by the writer[7,8], together with hitherto unpublished data, are briefly summarized in this paper.

Examination of Museum Material.—Careful examination of the intestinal contents of five workers of each species of termites in the U. S. National Museum revealed that wherever protozoa were present wood was also present and, *mutatis mutandis*, protozoa were present only when wood was present; thus confirming Imms' postulatum. Four families of termites are known. Among the 18 genera and 64 species examined from the family Termitidae, protozoa and wood were present in only 1 of the 21 species of the genus *Nasutitermes* and 2 of the 8 species of the genus *Mirotermes;* but protozoa and wood were present in 18 genera and 76 species,

or all that were examined, in the other three families (Mastotermitidae, Kalotermitidae, Rhinotermitidae). Thus the correlation between a strict wood-feeding habit and the presence of intestinal protozoa is perfect and positive.

Experimental Work on the Relation of the Protozoa to their Host: Material.—Living material of *Reticulitermes flavipes* Kollar, *Kalotermes schwarzi* Banks, *K. jouteli* Banks, *Prorhinotermes simplex* Hagen, *Termopsis nevadensis* Hagen and *T. angusticollis* Hagen was used in the experiments, although *R. flavipes*, owing to its local abundance, was used most extensively. The protozoa present in most of these termites, together with a classification of all the known termite protozoa, may be found in another paper.[7]

Removal of the Protozoa without Injury to the Host.—The feeding to termites of wood, antecedently soaked in aqueous solutions of various chemicals (NaCl, $CaCl_2$, $HgCl_2$, KCl, $CuSO_4$, etc.), resulted, as a rule, in killing both host and parasite if either was killed; on the other hand when humus, dirt, and cellulose were fed them, neither was killed. Many other methods were tried out, but cannot be given here.

Finally, however, it was discovered that if the termites were incubated for 24 hours at 36° C. all the protozoa were killed, while the host remained active and apparently uninjured. Termites from which the protozoa have been removed are referred to as defaunated termites.

Observations and Experiments on Defaunated Termites.—If given their normal diet of wood, defaunated termites become less active, with considerably flattened abdomens, on or about the 10th day after incubation, and are dead within 3–4 weeks.

What is the cause of death, incubation *per se*, the removal of cellulose digesting bacteria and fungi, or the removal of protozoa? In order to answer this question the three factors involved were studied separately.

Some of the defaunated termites were fed fungus-digested cellulose and some were fed humus. In neither case did death result, as had previously occurred when they were fed wood; they were active and apparently normal after four months, at which time the experiments were discontinued, for it had been shown that incubation *per se* was not responsible for the termites death.

Since incubated termites do not die when fed fungus-digested cellulose, and since cellulose is the principal constituent of wood, the intestinal bacteria and fungi of termites were carefully studied in all the media that have been used in the study and isolation of cellulose digesting microörganisms; but it was never possible, after many trials, to get any of these organisms to grow on any medium where cellulose was the only carbohydrate present. It was, therefore, concluded from this that the intestinal bacteria and fungi of termites do not aid their host in the digestion of cellulose. That unincubated termites are able to utilize cellulose was demonstrated

by the fact that they were active and apparently normal in every way after having been fed pure cellulose for four months; whereas when fed nothing, but kept under identical conditions of moisture, light and temperature as when fed cellulose, they died in 3–4 weeks.

Only the protozoa are now left to consider, and it is important here to note that they are very abundant, both in form and number, and *completely* fill the large and much distended gut of their host. In order to determine whether or not the removal of the protozoa by incubation was in any way responsible for the death of their host, several thousand incubation defaunated termites, with their right antennae cut off close up to the head, were placed in jars and vials, 10–50 in each, and were fed either wood or pure cellulose. In half the jars and vials the same number of unincubated termites were placed with the incubated ones. The incubated termites were killed and carefully examined at intervals of 1–30 days to determine whether or not they were being reinfected with protozoa; and it was found that they were regaining a protozoan infection from their associates, the number of protozoa present in them gradually increasing up to about the thirtieth day, at which time, in most instances, the usual number present in a single unincubated host had been attained. The incubated ones were removed from the unincubated at intervals of from 10–30 days and were seemingly normal after having been fed wood or cellulose for three months, at which time the experiments were discontinued, since it was evident that association with the unincubated for ten days or more had in some way restored the ability to utilize wood or cellulose as food.

But how had the incubated termites, by association with the unincubated ones, recovered their ability to live on wood or cellulose? Are the protozoa responsible? If so, how? This was studied in several ways. (1) The termites were wood starved, and it was noticed, after four to five days, that *Trichonympha*, the large and principal wood-ingesting protozoan in many termites, had disappeared entirely; after seven to eight days practically all the wood-ingesting species of protozoa were dead, while the non-wood-ingesting ones were as abundant as ever. These termites, though active and apparently normal, when returned to a wood diet lived but little, if any, longer than the incubation defaunated ones. (2) Several hundred adult individuals of the second form caste were isolated from many different colonies. These when fed wood or cellulose, in every instance, were all dead in 3–4 weeks. Adults of this caste do not harbor protozoa and eat wood rarely, if at all. They are fed salivary secretions by other members of the colony. (3) Adult soldiers harbor protozoa and have wood in their guts, but die when placed to themselves and given wood or cellulose, apparently because they cannot eat the food. They partake principally—entirely unless they eat wood meal—of proctodael food (wood)

furnished by other members of the colony. Protozoa, then, it seems must be present in order for a termite to live on a diet of wood or cellulose.

The next question to consider is, how do the protozoa function in enabling their host to live on wood or cellulose? The second form caste individuals that were isolated and studied did not eat the cellulose (Whatman filter paper No. 43), and, so far as I could tell, they never ate the wood either, for none was ever present in their guts. It is possible that the degeneration of the jaw muscles which occurs in this caste does not permit the eating of wood after reaching the adult stage, although it is certain that at an earlier stage in their life-cycle they did eat wood and were infected with potozoa, which are gradually lost, when their host, owing to the degeneration of its jaw muscles, ceases to furnish them with wood for food.

There is thus a very close correlation between the wood-feeding habit and the presence of intestinal protozoa. The protozoa are never present except when wood or cellulose is the principal food of their host. This close correlation of wood with the presence of protozoa, in species, castes, and even in the life-cycle of an individual in nature, strongly suggests that the protozoa in some way are directly connected with the utilization of wood as food, either by themselves or in coöperation with their host.

The protozoa probably use the wood as food and subsist on it largely rather than the intestinal fluids of their host, since they die 10–20 days in advance of the termites during wood starvation. Termites from which the protozoa have been removed by incubation or wood starvation, cannot live on a diet of wood, though they eat great quantities of it as may be seen by watching them or by a microscopic examination of their intestinal contents. In termites that have not been wood starved at all, certainly a very large percentage of the wood which they have eaten may at all times be found in the bodies of their intestinal protozoa; whereas in termites that have been wood starved for a few hours, it is almost impossible to find wood particles free in their intestines, because the protozoa have ingested them. Also when termites are wood starved, the amount of wood present in the protozoa gradually disappears.

All the microchemical tests that have been made to determine whether or not the protozoa digest the wood particles cannot be given here. A large quantity of glycogen is present in the bodies of the wood-ingesting protozoa, while none is present in the intestinal cells of the termites or in the non-wood-ingesting protozoa. This indicates that the wood-ingesting protozoa form the glycogen themselves. When the host has been fed nothing but the purest filter paper (.00006% ash) for three months, the wood-ingesting protozoa still have great quantities of glycogen present in their bodies, which suggests that they possibly split the cellulose into cellobiose, and the cellobiose into glucose from which they build up the glycogen.

The protozoa, but not the termites, it seems have the ability to digest wood or cellulose, which explains why the termites die, though given their normal diet, when the protozoa are removed from them, and why they live indefinitely when the protozoa are restored. It is quite probable, then, though not proved perhaps beyond all question, that the protozoa play a very important rôle in the digestion of the wood which their host eats, and that the relation of termites to their intestinal protozoa is one of symbiosis, the termites furnishing food and lodging for which the protozoa give them in return products elaborated from the wood.

[1] *Acknowledgment.*—Some of the investigations summarized in this paper were carried out after the writer was granted a Fellowship in the Biological Sciences by the National Research Council.

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THE ABSOLUTE WEIGHT OF THE HEART AND THE SPLEEN[1]

BY RAYMOND PEARL AND AGNES LATIMER BACON

SCHOOL OF HYGIENE AND PUBLIC HEALTH, JOHNS HOPKINS UNIVERSITY

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In some earlier work the authors[2] found that the organ weight ratios L/H, K/H, L/S, H/S, and K/S (where L denotes liver weight, H heart weight, K kidney weight, and S spleen weight) had values which suggested that, in persons whose only significant pathological lesions at autopsy were those of tuberculosis, the weight of the heart was relatively low and that of the spleen relatively high. It was determined to make a thorough study of the absolute weight of those two organs, from the same material used in the earlier study. This tedious task has now been completed. In advance of the final publication of the results[3] in a place perhaps not generally accessible to non-medical readers, it seems desirable to make a brief report of the work here.

The method used in this work for comparing different groups in respect of the absolute weights of organs, which change in size with age, as a result both of processes of growth and of senescence, seems worthy of mention. It consists essentially of setting up and measuring as wholes *difference bands*

between the regression lines of the organ upon age in each of the compared groups. As developed in this investigation the method appears to have some points of novelty. At least we are not aware of its application hitherto to a biological problem which, in one way and another, has been much discussed in the literature. The extensive trial of the method which has been made in this study has convinced us of its essential soundness and usefulness. For details the complete memoir must be consulted.

The *regression of heart weight upon age* is non-linear, taking the whole life span together. The absolute weight of the heart is found to be notably

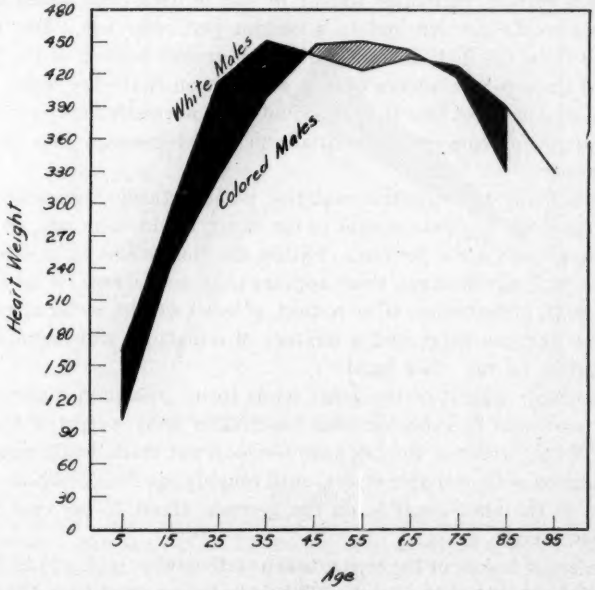

FIGURE 1

Regression lines, and difference band, for heart weight upon age in a group of colored and white males, in which each person showed at autopsy other significant lesions besides those of tuberculosis. On the portion of the difference band which is solid black the white line lies above the colored, and in the cross-hatched portion the colored line lies above the white.

larger at each age from birth up to an age somewhere between 35 and 55, and then steadily but more gradually to be of lower weight with advancing years, until the upper end of the life span is reached. This curvilinear form of the regression line of which a typical example is shown in figure 1, is essentially the same whether the heart itself displays pathological lesions or does not; in the two sexes; and in the white and colored races. The existence of this orderly relationship between heart weight and age shows

how futile are such statements as: "The average weight of the adult heart is *m* grams." Unless one knows how many hearts of each different age went into the making of the average, the result is meaningless. It is emphasized in the body of this paper that the inference, from such statistical regression lines as those here dealt with, of corresponding weight *changes* during the life history of any particular individual heart is not, in strict logic, justifiable. All the statistically observed phenomena would be the same if the heart neither increased in weight during growth, nor decreased during senescence, if it were the fact that the possession of a heart of a certain particular weight in and of itself determined that the individual would survive just to a certain particular age. But this we know *not* to be the fact, at least during the growth portion of the life history, and there is no evidence of it in any portion of the life span. There is no reasonable doubt that the individual heart normally *changes* its weight at ages according to a curve essentially like the regression lines presented in this study.

There is found to be, in this material, no statistically significant difference in the mean absolute weight of the heart, at the same age, *in colored as compared with white persons*. Within the limitations of this material as a basis for generalization, there appears to be no warrant for an assumption of racial differentiation in respect of heart weight, so far as concerns whites, on the one hand, and a mixture of mulattoes and perhaps a few pure negroes, on the other hand.

The absolute weight of the heart tends to be greater in males than in females, as would be expected from the greater body weight of the male. But the *sex difference in absolute heart weight* is not statistically significant, in comparison with probable errors, until roughly age 25 is reached. From that age on the male heart is, on the average, about 25 per cent heavier than the female heart.

The effect of *lesions* of the organ, taken statistically, is clearly to increase the absolute weight of the heart. This is to be expected from the general consideration that the heart tends to compensate for any fundamental derangements of its organization by increasing its size.

There is a distinct tendency for the heart to be smaller in the group of cases where the lesions of *tuberculosis* were the only significant deviations from normality found at death. In other words, where tuberculosis alone kills, the heart tends definitely to be smaller than in cases where other pathological conditions are partly resposible for the death. This result is, in general, true regardless of sex or age, or presence or absence of heart lesions. In magnitude the differences in heart weight associated with degree of importance of the tuberculous process, are small and statistically insignificant in comparison with probable errors in early life, and large and generally significant statistically in later life.

The regression of spleen weight upon age is highly non-linear. The spleen weight is found to be progressively larger as age advances, up to the decade centering at 35 years, and to become progressively smaller at the more advanced ages thereafter. The ascending and descending limits of this regression curve appear to be, in this experience, nearly straight lines; or at the most only slightly curved. The contrast between this inverted V type of regression line seen in figure 2 and the smooth curve of the heart weight regression is great.

The absolute weight of the *spleen* is definitely greater in the *white* than

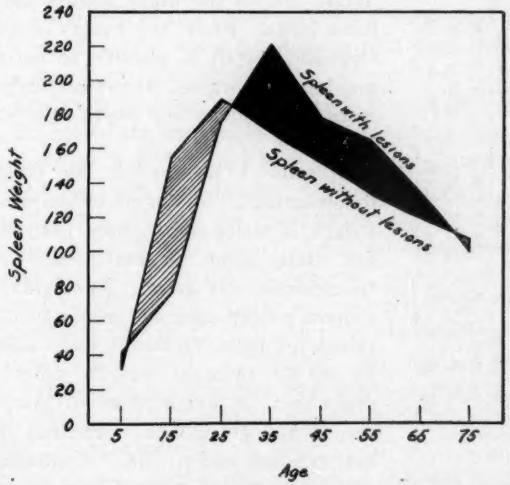

FIGURE 2

Regression lines, and difference band, for spleen weight upon age in group of colored males, in which each person showed at autopsy other significant lesions besides those of tuberculosis.

it is in the *colored* group. This finding is in agreement with that of other workers on the same point.

There is a definite tendency for the *female spleen to be larger than the male* up to age 10. After that age the male spleen has the higher absolute weight, as would be expected. In general, however, the difference between the sexes in spleen weight are not large enough to be significant in comparison with their probable errors. The sex differences in spleen weight tend to be larger in colored than in whites.

In general the *lesioned* spleen is heavier than the *non-lesioned*.

There is a tendency for the spleen, particularly the non-lesioned spleen, to be *heavier* where *tuberculosis* is the only significant pathological condition.

TABLE 1

COMPARISON OF NON-LESIONED HEART WEIGHTS IN THE TUBERCULOSIS ONLY GROUP, WITH THOSE OF NORMAL NON-TUBERCULOUS PERSONS (VIERORDT'S AND OPPENHEIMER'S DATA)

MID-AGES	SMOOTHED MEANS. TUBERCULOSIS ONLY. NON-LESIONED HEARTS.		WEIGHTED MEANS FOR INDICATED AGE GROUPS					
	WHITE AND COLORED TOGETHER		WHITES ONLY		VIERORDT'S NORMAL DATA		OPPENHEIMER'S ACCIDENT CASES	
	MALES	FEMALES	MALES	FEMALES	MALES	FEMALES	MALES	FEMALES
5	66.7 (30)	61.2 (34)	75.0 (12)	58.6 (14)	49.7 (252)	51.1 (296)	87.9 (7)	55.0 (3)
15	157.0 (13)	135.8 (21)	151.1 (3)	145.3 (2)	220.7 (107)	243.4 (89)	264.4 (9)	241.8 (20)
25	235.5 (42)	210.7 (17)	221.5 (11)	237.0 (6)	302.9 (143)	257.5 (139)	337.6 (28)	272.1 (7)

Throughout the work the desirability of comparing the weight of the heart and spleen in the tuberculosis only group of cases, with their weight in a group of cases where there was no tuberculosis. Our own researches on the Johns Hopkins Hospital pathological data have not yet reached a point where this is possible. By going to the organ weight literature we can, however, make such comparisons up to age 25, though unfortunately not for the whole span of life, on any reliable basis. From the papers of Vierordt[4] and Oppenheimer[5] it is possible to extract data for non-lesioned organs, in persons dying from diseases or accidents in which no tuberculosis is involved.

In table 1 we present for comparison the following data: (*a*) our smoothed means for heart weight, of males and females, both races together and whites alone, for non-lesioned hearts in the tuberculosis only group; (*b*) weighted mean heart weights for the same age groups as in our material calculated from Vierordt's basic tables (*loc. cit.*, pp. 89–90) of organ weights collected from the literature; (*c*) weighted mean heart weights for the same age groups calculated from Oppenheimer's (*loc. cit.*, p. 348) "Unglücksfälle" table. All cases of "wasting diseases" and especially tuberculosis are excluded from these data, and so far as known to the compilers, only non-lesioned organs are included.

From table 1 we note that:

1. Except in the lowest age group the heart weights in the tuberculosis only group are well below those in either of the non-tuberculous series. In the decade of life centering at age 5 the weights are practically the same in all three series. These results may be taken as practically conclusive evidence that the diminished weight of the heart in the tuberculous is the direct effect of the disease in the individual, and does not represent merely an effect of pathological selection as suggested in Pearl and Bacon,[2] p. 225. In the first age group the weights are the same for the reason that

in infancy and early childhood killing tuberculosis is, generally speaking, so rapidly fatal an acute disease that there is not time for a significant wasting effect upon the heart muscle. It is doubtful if the difference band between heart weight of tuberculous and non-tuberculous has reached its maximum at age 25. Unfortunately it is impossible from lack of data to be sure on this point. It was shown by Reuter[6] many years ago, that in the phthisical the right ventricle was hypertrophied (because of the diminished lung circulation according to Grober[7]) and the left ventricle greatly atrophied. As the bulk of the heart's weight is of the left ventricle the findings here accord well with those of Reuter.

2. A study of the data of this paper makes it seem certain that Oppenheimer[5] and Vierordt[4] are in error in assuming that the normal growth of the heart has been completed by age 25. As a matter of fact the true age of maximum heart weight is probably nearly if not quite 10 years later.

In case of the spleen the material is meager except for Vierordt's series. So far as the data go, however, they give no support for the view, tentatively suggested by Pearl and Bacon,[2] that the spleen is significantly heavier in the tuberculous than the non-tuberculous. In the two groups centering at ages 5 and 25, there is no substantial difference between the values of spleen weight for our tuberculosis only group, and either of the two non-tuberculous groups. In the group centering at age 15 the values in our series are distinctly lower, but the series are so small, that no weight can be attached to the result. Altogether, the question must still be left open, with the distinct probability that it will be found that there is no significant difference in the absolute weight of the spleen in the tuberculous and the non-tuberculous.

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THE NATURE OF RESISTANCE TO SEEDLING BLIGHT OF CEREALS[1]

BY JAMES G. DICKSON, SOPHIA H. ECKERSON, AND KARL P. LINK

UNIVERSITY OF WISCONSIN AND OFFICE OF CEREAL INVESTIGATIONS, BUREAU OF PLANT INDUSTRY, UNITED STATES DEPARTMENT OF AGRICULTURE

Read before the Academy, April 23, 1923

The seedling-blight of wheat and other cereals, caused by *Gibberella saubinetii* (Mont.) Sacc., has proved to be especially well adapted to a critical study of the relation of environment to parasitism and predisposition to disease, for the reason that the same parasite is able to attack a number of different host plants, which vary greatly in their responses to at least one environmental factor, soil temperature. Field observations on wheat and corn during the past four years have indicated that soil temperature and soil moisture are important factors in the development of this

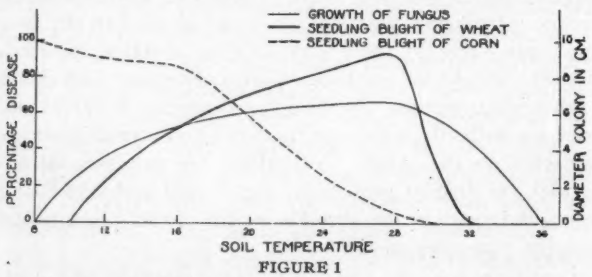

FIGURE 1

Curves comparing the influence of incubator temperature upon the vegetative development of the parasitic Fusarium in culture, with the influence of corresponding soil temperatures upon the development of the Fusarium blight in wheat and corn seedlings. Note that in wheat, the curve for the development of the disease parallels that for the development of the fungus, whereas, in corn it is practically the reverse of that for the development of the fungus. It seems logical to conclude, therefore, that the dominant influence of temperature upon disease development is primarily upon the hosts rather than upon the parasite. This is illustrated more graphically in the next figure.

disease. As a result of the suggestions from these field observations and the apparent importance of the diseases on both wheat and corn, investigations were undertaken to determine the relation of soil temperature and soil moisture to the development of seedling blight of wheat and corn caused by *Gibberella saubinetii*. The responses of the two hosts, wheat and corn, were so markedly different[2] that the studies were continued with the view of determining the physiological and chemical responses which de-

termine host susceptibility. Although the results here summarized are not complete, it is believed that they will serve to show the relation of soil temperature and moisture to the predisposition of wheat and corn to this seedling blight.

This disease is manifest on both wheat and corn, first, by blighting before germination or before emergence, which results in poor stand and, second, by blighting after emergence, which is evident by the yellowed and wilted seedlings. The invaded tissues in both hosts become reddish-brown to carmine red, depending upon environmental factors.

The parasite in pure culture functions normally over a comparatively wide range of temperature, namely, from 3° to 32° C. The optimum temperature for spore germination, vegetative development, and sporulation, is about 24° to 28° C.

The wheat plant functions best in all stages of its development at relatively low soil temperatures. While wheat germinates more rapidly at soil temperatures of 24° to 28° C., the germination is more uniform and stronger plants are produced at the lower soil temperatures—about 8° to 16° C. On the other hand, corn seedlings develop best at soil temperatures of 24° to 28° C. Uniformity of germination and stand diminish rapidly below 20°, while at 12° and below all growth processes are greatly retarded.

The marked difference in the development of wheat and corn at different soil temperatures together with the ability of the fungus to grow at a wide range of temperatures offers an exceptional opportunity, therefore, to compare the influence of soil temperature upon the possible parasitic attack and resultant disease development in these two cereals. If soil temperature is a controlling factor in the development of seedling blight, is it primarily due to the influence of temperature on the host or parasite? If upon the fungus, then blighting of wheat and corn alike should be more severe at the relatively high soil temperatures which favor development of the fungus. If upon the hosts, then the reaction of wheat should be different from that of corn.

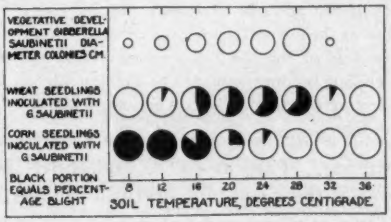

FIGURE 2

A graphic summary of the vegetative development of the seedling blight fungus in artificial culture and the comparative quantities of seedling blight of wheat and corn at different soil temperatures. The black portion of the circle shows the average percentage of blighted seedlings. Shown in more detail in figure 1.

The seedling blight of wheat develops only on the seedlings growing at the higher soil temperatures. The plants grown in the greenhouse at

8° C. and in the field when the mean soil temperature is below 10° C., do not blight. Above 10° C., blighting appears and increases rapidly in severity with rising soil temperatures up to about 20° to 24° C., which is the maximum temperature for the production of seedling blight. Thus the temperature curve for the seedling blight of wheat seems to parallel closely that for the growth of the fungus (Fig. 1). The natural suggestion, therefore, is that the blight is caused by the stimulating influence of the higher soil temperature on the fungus. On the other hand, the experiments show that low soil temperatures favor wheat development at all stages of growth, whereas, the high soil temperatures produce weak, abnormal plants. Before drawing conclusions, therefore, consideration should be given to the relation of soil temperature to disease development in corn, which is a relatively high temperature plant.

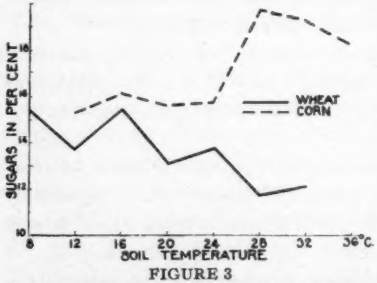

FIGURE 3

Curves showing the influence of soil temperature upon the sugar content of wheat and corn seedlings at emergence. Note that in the wheat seedlings with the rise in soil temperature there is a gradual decrease in amount of sugars available for building cell walls, whereas, in the corn seedlings the available amount of sugars are relatively low at the low soil temperatures and increase twofold at the soil temperature where the seedling becomes resistant to seedling blight. Compare with the dextrin content as shown in figure 4.

The seedling blight of corn develops on the seedlings growing at the low soil temperatures. At 8° C., where all the wheat plants remain disease free, all of the corn seedlings blight. The disease is severe at temperatures from 12° to 16° C., and milder at those from 16° to 24° C., where it is checked entirely, only a few root lesions resulting. Thus at 24° C. and above the parasite does not attack corn and yet at these soil temperatures the seedling blight of wheat is very severe. These results are shown graphically in figure 2. Consideration of these results shows at once that the dominant influence of soil temperature must be with the hosts rather than with the parasite. This is further shown by the results obtained with soil moisture experiments.

Lowering the soil moisture to a point where the normal metabolism of the seedling is inhibited predisposes both wheat and corn seedlings to attack by the seedling blight organism. The seedlings of both wheat and corn are blighted at all soil temperatures when the moisture content of the soil is reduced to 30 per cent of the moisture-holding capacity. Control plants growing in sterilized soil are equally vigorous at the low and the high soil moistures. In contrast, the plants growing in the disease-infested soil blight severely with low soil moisture, at all soil tempera-

tures. In other words, with low soil moisture, wheat seedlings growing at 8° C. blight severely and corn seedlings growing at 24° C. blight badly.

It seems then that conditions of environment, whether of temperature or moisture, which are unfavorable for the best development of the cereal seedling, predispose it to attack by the fungus. The natural inference is that it may be due to some disturbance in the normal metabolism of the plant. The influence of illumination also was determined and the results further support the above inference. For example, at a soil temperature of 10–12° C., which is about the critical soil temperature for the production of blight, wheat seedlings grown with a low light intensity blight badly, whereas series grown with a higher light intensity and with a longer period of illumination each day do not blight.

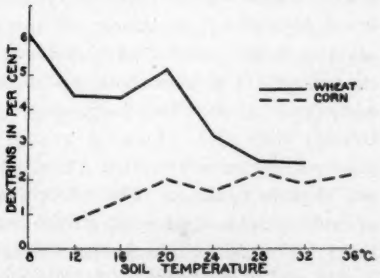

FIGURE 4

Curves showing the influence of soil temperature upon the dextrin content of wheat and corn seedlings at emergence. Note that in wheat seedlings there is an unusually high dextrin content at 8° C. where the wheat seedling is resistant to seedling blight and a rapid decrease with the rise in soil temperature. Compare this curve with that for the sugar content of corn in figure 3. There is a gradual rise in dextrin content of the corn seedlings with the rise in soil temperature. Compare this curve with that for the sugar content of wheat in figure 3. These analyses indicate that in wheat the dextrin content changes rapidly with soil temperature changes, whereas, in corn the sugar content fluctuates with soil temperature changes. The rapid increase in these substances occurs in wheat and corn respectively at the same soil temperatures as resistance to seedling blight.

Studies on the character and extent of the fungus penetration of the host under these different environmental conditions show that an important relation exists between host-tissue composition and disease development. For example, in the wheat seedlings growing at the low soil temperatures, the fungus hyphae slowly penetrate between the cell walls of the tissues, whereas, at the high soil temperatures, direct and rapid cell penetration occurs. On the other hand, in the corn seedlings growing at the low soil temperatures, direct penetration of the cell walls occurs, in contrast with a slow invasion between the cell walls of these tissues at the high soil temperatures. In both wheat and corn seedlings all gradations between these two types of penetration occur at the intervening soil temperatures.

These experiments indicate, further, that soil temperature and other environmental factors, acting over periods of considerable duration, are more influential than brief exposures to extremes in determining predisposition to disease. Therefore, fungus penetration and disease development,

or "blighting," probably are associated with the growth responses of the hosts. If this be true, the nature of disease resistance or disease susceptibility can best be determined by a study of the influence of environment upon the plant metabolism. The metabolism of the germinating wheat and corn seedlings, as shown by microchemical and analytical chemical determinations, is sufficiently different at the various soil temperatures to explain in a large part the difference in response of the two plants.

At the low soil temperatures, the starch in the wheat endosperm is hydrolyzed much more rapidly than the protein. At the end of seven days at 12° C. nearly all the starch from the lower flanks of the grain is hydrolyzed. There is much sugar in the embryo, especially in the growing root, coleorhiza, and coleoptile. The storage protein in the endosperm is only just beginning to be hydrolyzed and that at an extremely slow rate. There is a little peptone in the endosperm, but no amino acids can be detected. The cell walls of the coleorhiza are of cellulose and slightly lignified. The coleoptile epidermis is cutinized.

Under similar conditions of light and moisture but at higher soil temperatures, 25° to 32° C., both starch and protein are hydrolyzed very rapidly. At the end of two days at 24° C., much of the starch of the endosperm is hydrolyzed and also all of the protein from the lower half of the grain. The embryo contains some glucose, considerable dextrin, and many small starch grains in the cells of the coleoptile and the root sheath. Some asparagin and other amino acids are present in the region of the first node. The cell walls are chiefly of pectic substance. There is no cellulose in the cell walls of the root sheath, except in the walls of the coleorhiza hairs. The cuticle of the coleoptile is of cellulose. There is no cutinization or suberization.

This study of the cell walls of the germinating wheat embryo indicates that their chemical nature depends upon the kind of building materials available and their proportion, one to another. In the very early stages of growth of the embryo this proportion depends largely upon the relative rates of hydrolysis of the stored starch and protein at any specific temperature. Because there is an abundance of sugar and extremely little available protein material in the embryo during the first ten or twelve days at the low soil temperatures, these young seedlings are practically high-carbohydrate plants, having thicker and more resistant cell walls, while at high temperatures the embryos are relatively high in protein, even at the end of twenty-four hours. There is more rapid vegetative growth, therefore, and less of the carbohydrate is used in building and thickening the cell walls.

Quantitative chemical analyses agree with the microchemical study of the wheat seedling and further indicate decided differences in the metab-

olism of the corn seedling. At the low soil temperatures, the wheat seedlings, separated from the endosperm, are high in sugars; 15.5 per cent at 8° C. in contrast with 11.9 at 28° C. Likewise, the dextrins in the wheat seedling are highest at the low temperatures; 6.1 per cent at 8° in contrast with 2.5 per cent at 28° C. On the other hand, at the low soil temperatures, the corn seedlings separated from the endosperm are low in sugars; 15.4 per cent at 12° in contrast with 19.9 per cent at 28° C. Likewise the dextrins in the corn seedling are lowest at the low temperatures 0.8 per cent at 12° in contrast with 2.2 per cent at 28° C. (Figs. 2 and 3.)

The relative high content of available carbohydrates in the wheat seedling at the low soil temperatures and the corn seedling at the high soil temperatures results in thickened cellulose walls offering resistance to fungus penetration. Undoubtedly this difference in chemical composition likewise supplies a different medium for fungus growth when penetration does occur.

A better understanding of the intricacies of parasitism can best be obtained by studying the influence of environment upon the metabolism of host and parasite alike. This must eventually lead to an explanation of the nature of disease resistance and the influence of environment upon the expression of resistance factors in plants.

[1] For a more general introduction to the work on disease resistance in plants at the University of Wisconsin, see the article "Disease Resistance in Cabbage," by L. R. Jones, *Proc. Nat. Acad. Sci.*, **4**, p. 42, 1918.

[2] For a more detailed consideration of this phase of the problem reference may be made to *J. Agr. Res.*, **23**, 837–870, 1923, "Influence of Soil Temperature and Moisture on the Development of Seedling Blight of Wheat and Corn Caused by *Gibberella saubinetii*," by James G. Dickson.

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